Aquat. Living Resour. 18, 361–372 (2005)

DOI: 10.1051/alr:2005039
www.edpsciences.org/alr

Aquatic
Living
Resources

The spatio-temporal pattern of Argentine shortfin squid *Illex argentinus* abundance in the southwest Atlantic

Mar Sacau[1,a], Graham J. Pierce[2], Jianjun Wang[2], Alexander I. Arkhipkin[3], Julio Portela[1], Paul Brickle[3], María B. Santos[1,2], Alain F. Zuur[4] and Xosé Cardoso[1]

[1] Instituto Español de Oceanografía, PO Box 1552, 36200 Vigo, Spain
[2] Department of Zoology, School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen, AB24 2TZ, UK
[3] Fisheries Department, Falkland Islands Government, PO Box 598, Stanley, Falkland Islands
[4] Highland Statistics Ltd., 6 Laverock Road, Newburgh, Aberdeenshire, AB41 6FN, UK

Accepted 21 July 2005

Abstract – The Argentine shortfin squid (*Illex argentinus*) is a common neritic species occurring in waters off Brazil, Uruguay, Argentina, and the Falkland/Malvinas Islands in the southwest Atlantic. *Illex argentinus* is the most important fished cephalopod species in the area and plays a significant role in the ecosystem. It is object of major fisheries using both trawlers (mostly from European countries) and jigging vessels (mainly from Asian countries) and estimated total annual average catch for the last 15 years (1988-2003) is about 700 000 tons. The present paper aims to develop predictive models of squid abundance in relation to physical and environmental conditions, models that could ultimately be applied to fishery forecasting. Fishery and biological data collected by scientific observers aboard commercial trawlers between 1988 and 2003 were analysed in relation to physical and environmental factors to establish the spatio-temporal pattern of the species' distribution and quantify the influence of environmental variables (e.g. SST, depth) on local abundance. The data included 26 168 fishing haul records, of which 11 103 were positive for *Illex*. CPUE (Catch Per Unit Effort, kg h^{-1}) was used as abundance index. The analyses were based on time-series maps created using Geographical Information Systems (GIS). GIS maps showed that highest CPUE values were recorded during the first four months of the year (the Austral summer-autumn), with peak values higher than 5000 kg h^{-1} mainly located within 42° S, 46° S and MN (North part of Malvinas/Falkland) areas. Generalised additive models (GAMs) were used to describe variation in *Illex argentinus* abundance in relation to geographical and environmental variables. The presence/absence (PA) of *Illex* and its abundance (CPUE) in areas of presence were modelled separately. Predictors retained in the optimal models included SST, latitude, longitude, month, average fishing depth and year. Both models suggest a clear seasonal effect: maximum catchability was found during March (PA model) and the maximum abundances were found during the first quarter of the year (CPUE model). GAM models also demonstrated that higher catches and maturity of squid were related, in general terms, to warmer and deeper water.

Key words: Argentine shortfin squid / *Illex argentinus* / GIS / GAM / Environment / Spatio-temporal pattern

Résumé – Abondance spatio-temporelle du calmar *Illex argentinus* dans l'Atlantique Sud. L'encornet rouge argentin (*Illex argentinus*) est une espèce néritique commune de l'Atlantique Sud-Ouest présente dans les eaux du Brésil, de l'Uruguay de l'Argentine et des îles Malouines (Falklands). *Illex argentinus* est la principale espèce de céphalopode exploitée dans cette région où elle joue un rôle majeur dans l'écosystème. L'espèce est pêchée par d'importantes flottilles de chalutiers (principalement de pays européens) et aux turluttes industrielles (de pays asiatiques) pour une production annuelle de 700 000 t en moyenne sur les 15 dernières années (1988-2003). Cet article présente des modèles prédictifs de l'abondance en fonction des facteurs physiques et environnementaux ; modèles qui pourraient à terme être appliqués à la gestion des pêches. Les données de capture et les paramètres biologiques récoltés, grâce à des observateurs embarqués, de 1988 à 2003, ont été analysées en relation avec les facteurs physiques pour préciser les variations spatio-temporelles de répartition et quantifier l'effet de la température et de la profondeur sur l'abondance. Le jeu de données porte sur 26 168 traits de pêche dont 11 103 comportant des captures d'*Illex*. Les captures par unité d'effort (CPUE en kg h^{-1}) sont utilisées comme indice d'abondance et les analyses utilisent des séries de cartes, créées avec un système d'information géographique (SIG). Les valeurs les plus élevées de CPUE sont enregistrées durant les quatre premiers mois de l'année (l'été et l'automne austral) avec un pic dépassant 5000 kg h^{-1} localisé

[a] Corresponding author: mar.sacau@vi.ieo.es

entre 42° S et 46° S dans la partie Nord des Malouines. Les modèles additifs généralisés (GAM) ont servi à décrire les variations d'abondance en fonction des variables géographiques et environnementales. La présence ou l'absence de la ressource est modélisée séparément de l'abondance. Les modèles optimaux retiennent comme variables explicatives la température, la latitude, la longitude, le mois, la profondeur et l'année. Les deux modèles indiquent un effet saisonnier net: la capturabilité est maximale en mars (présence/absence) et l'abondance (CPUE) est la plus élevée durant le premier trimestre. Les modèles additifs généralisés montrent également que les captures les plus élevées d'animaux à maturité sont associées à des eaux plus tièdes et des secteurs plus profonds.

1 Introduction

The Argentine shortfin squid (*Illex argentinus*) is a common neritic species occurring in waters off Brazil, Uruguay, Argentina, and the Falkland/Malvinas Islands in the southwest Atlantic (Nesis 1987; Arkhipkin 2000), where it is the most important cephalopod species in fisheries and plays a significant role in the ecosystem. Like many other cephalopod species it has an annual life cycle (Hatanaka 1986) and is migratory (Caddy 1983).

The life-cycle of *Illex argentinus* is associated with the subtropical confluence of the Brazil and Falkland (Malvinas) Currents (Fig. 1) during reproduction and the early life stages (Hatanaka 1988; Brunetti and Ivanovic 1992; Rodhouse et al. 1995; Haimovici et al. 1998) and with the Falkland (Malvinas) Current over the Southern Patagonian shelf during maturation, feeding and growth (Rodhouse et al. 1995).

Concentrations of shortfin squid are found 45–46° S in January or February and the animals subsequently migrate southward towards the Falkland Islands while growing rapidly. Peak concentrations are found around the Falkland Islands between March and May. Toward the end of this period, animals start migrating northward, ultimately to spawn and die in shelf and slope waters off northern Argentina, Uruguay and Brazil around July or August (Brunetti 1988; Santos and Haimovici 1997; Basson et al. 1996; Portela et al. 2002).

The marine environment off austral South America is rich in coastal fronts. Spawning of the squid *I. argentinus* is associated with these fronts. The shelf-break front is a permanent feature that characterizes the border of the shelf. The inner boundary lies between the 90 and 100 m isobath. During the austral summer the front presents mild gradients in the density and thermal fields but is weak in the salinity field. During winter, salinity alone controls the density gradient. The gradients are strongest during autumn (Martos and Piccolo 1988). The geographical location of the front may vary according to the dynamics of the Falkland (Malvinas) Current, for which cyclical variations – including semi-annual, annual and biannual periods – have been reported (Acha et al. 2004).

The fishing grounds in the Patagonian Shelf in which vessels flying Spanish flag are operating can be divided in two main fishing zones, one of them around the Falkland/Malvinas Islands in what are known as Falkland Interim and Outer Conservation Zones (FICZ and FOCZ respectively), and the second one in the "High Seas" (Fig. 2).

The activity of Spanish vessels in the High Seas is restricted to those portions of the continental shelf and slope which fall outside the Argentinean EEZ, i.e. a small patch around 42° S and a bigger area between parallels 43° 30' and 48° S, namely "Area 42" and "Area 46" respectively. The fishing grounds around the Falkland Islands have been divided in three sub-areas: Malvinas North (MN), Malvinas West (MW) and Malvinas South (MS). Commercial fleets working in the area routinely carry fisheries observers, who record data on catches and associated conditions. Taking advantage of the availability of this large spatially and temporally referenced data set (1988-2003), the present paper aims to develop predictive models of squid abundance in relation to physical environmental conditions; models which could ultimately be applied to fishery forecasting. Additionally we used associated biological data to provide a detailed description of the relationships between growth, maturation and migrations.

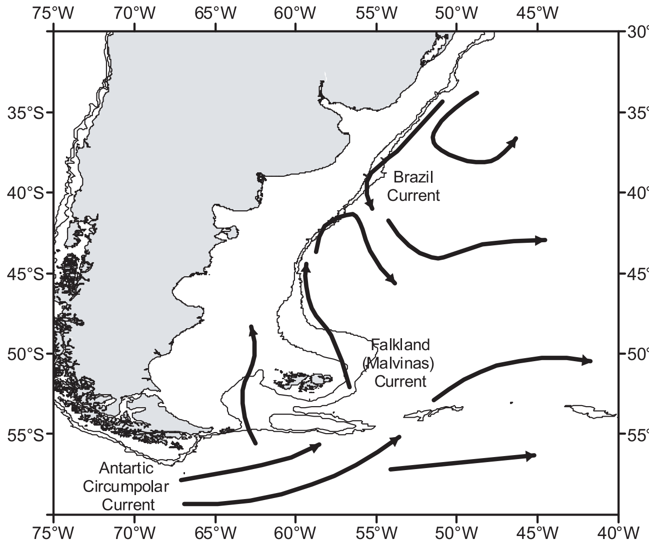

Fig. 1. Map of the study area showing the main current systems: the Antarctic circumpolar current, the Brazil current and the Falkland/Malvinas current.

2 Material and methods

2.1 Data sources: Fishery data

Daily fishery data were collected by observers working for the IEO (Instituto Español de Oceanografía, Vigo, Spain) and Falkland Islands Government Fisheries Department, Stanley, on board commercial vessels for the 17-year period 1988-2003, in the SW Atlantic fishery areas (Fig. 2). The inference of distribution patterns from commercial data requires some caution due to the fact that location of commercial trawls is influenced by a variety of considerations such as license conditions, vessel capabilities, commercial priorities and the knowledge and experience of the crew. Nevertheless, it is assumed that these data were representative of the fishery.

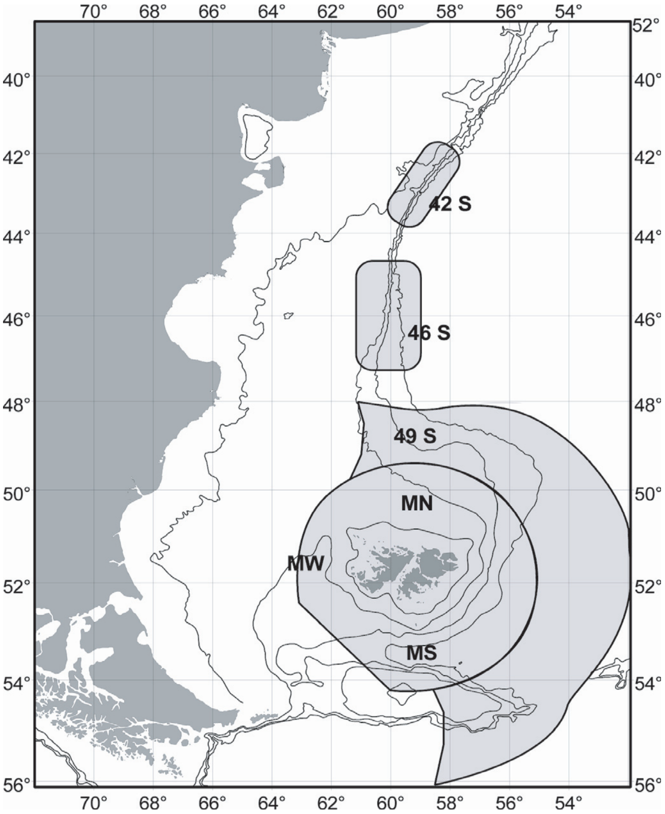

Fig. 2. Map of the study area showing the locations of the main fishing areas along the Patagonian Shelf for the Spanish fleet, also the boundaries of the Falkland Islands Conservation Zones. MN = Malvinas North, MW = Malvinas West, MS = Malvinas South; FICZ = Falklands Interim Conservation Zone; FOCZ = Falklands Outer Conservation Zone. The map also shows depth contours (100, 200, 500 and 1000 m).

The Spanish fishing fleet operating in the SW Atlantic is mainly based in Vigo harbour (Spain). Nowadays this fleet comprises around 25 freezer vessels, typically about 1000 GRT, 60−65 m in length and with 2000 hp engine power. Between 1983 and 2004 the fleet of the main Spanish Shipowners Association (ANAMER) which represented around 75−90% of the total fleet, fluctuated in size between 18 and over 80 boats, with peak numbers in 1990 (Fig. 3).

Bathymetry contours for the Patagonian shelf were extracted from the GEBCO (General Bathymetric Chart of the Oceans) Digital Atlas. CPUE (catches per unit effort, kg h^{-1}) was used as an index of abundance in the fishery (Waluda et al. 1999). This index reflects squid abundance and accounts for changes in fleet activity over the 17-year period. Observers collected also supplementary data, i.e. main characteristics of every haul, environmental and physical data, comprising fishing location, fishing depth, tow time, SST, SBT, sea state, lunar cycle and sky state.

The catching power of individual boats is variable, it was considered to be impractical to attempt to apply correction factors. Therefore hours fishing is used as the index of effort. This could introduce additional noise into the data.

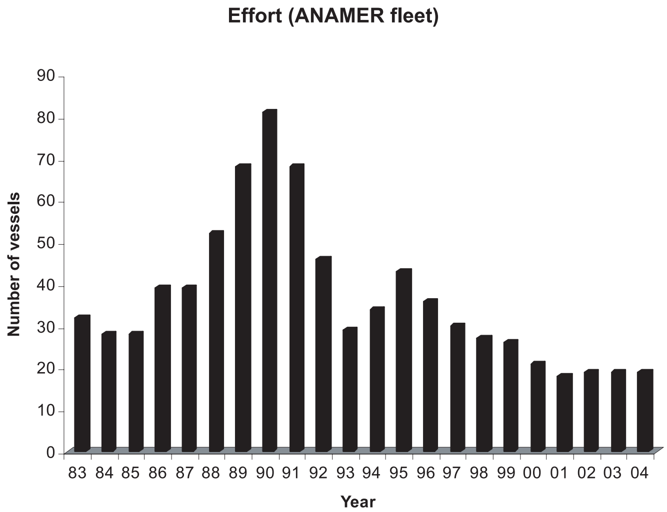

Fig. 3. The number of Spanish fishing vessels operating in Falklands and Patagonian Shelf area for the period 1983-2004.

All fishery and environmental data were integrated into a database (MS Access) and GIS (ArcGIS version 8.2) for use in analysis and modelling. GIS was used during exploratory analysis, complementing the use of scatterplots, to visualise the spatial component of relationships between *Illex* abundance and environmental variables.

2.2 Statistical analysis and modelling

Generalized Additive Models (GAMs) are able to deal with non-linear relationships between an independent variable and multiple predictors and are particularly appropriate to our study.

GAMs were first proposed by Hastie and Tibshirani (1990) and some of the first applications to fishery data were by Swartzman et al. (1992 and 1995). A GAM is a non-parametric regression method with less strict assumptions than linear regression. This method is an extension of the generalized linear models (GLMs; McCullagh and Nelder 1989). The principal strength of additive models is their ability to fit complex smooth functions (smoothers) to the predictors rather than being constrained by the parameterisation implicit in GLMs. A GAM, the generalized version of an additive model (relaxing the assumption that y has a Gaussian [normal] distribution), is expressed as:

$$g(E[y]) = \beta_0 + \sum_k S_k(x_k).$$

The right-hand side of the equation is the additive predictor. β_0 is an intercept term and S_k is a one-dimensional smoothing function for the k^{th} explanatory variable, x_k. The degree of smoothing is determined by the degrees of freedom (df) associated with the smoothing function. The larger the degrees of freedom, the less the smoothing performed and more flexible the function obtained. The function g is the so-called "link-function", essentially a transformation applied to the expectation of the y values.

To model variation in *Illex argentinus* abundance GAMs were fitted using the "gam" command in Brodgar software (Highland Statistics Ltd). All data were imported into Brodgar from Microsoft Excel data files and initially screened to reveal characteristics of data sets and detect outliers.

Because the CPUE data set contains a large number of zero values, models were fitted using a two-stage procedure. The first GAMs described factors affecting the binomial response variable presence/absence (PA). Secondly, for the subset of non-zero CPUE values, a quasi-Poisson distribution was assumed, accounting for the over-dispersed nature of the response variable (CPUE) data, and further GAMs were fitted. The link functions used to model responses were log [$f(z) = \log(z)$] and logit [$f(z) = \log(z/(1-z))$] for the abundance and PA models respectively. A cubic smoothing spline method was chosen to smooth the variables, using 4 degrees of freedom by default.

Models were constructed following a forward stepwise procedure, evaluating alternative models in terms of the Akaike Information Criterion (AIC). The explanatory variables used in these models included week, average fishing depth, SST, month, longitude, latitude, sky state, sea state and phase of the moon. Year was included in all models to explore interannual trends in abundance and presence/absence of *Illex argentinus*.

The GAM output plots show the smoothers for the effects of all the variables included in the model. The dotted lines represent the 95% confidence intervals. The density of tick marks on the x-axis (the rug) indicates the number of data points available for different values of x. Fewer points lead to wider confidence limits. The plots show the best fitting smoothers for the effect of the explanatory variables included in the model. The partial components, as represented by the y-values on the GAM plots, express the relationship between the link function of the response variable and each of the variables included in the model.

2.3 Analysis of biological data

Data on squid length (dorsal mantle length, DML) were collected by observers by for at least 75 individuals in each sample when possible. Maturity in the Argentine shortfin squid was recorded on a scale of six and five maturity stages for females and males respectively, based on differences in the appearance and size of the gonads and accessory glands. This scale is a modification of the one developed by Lipinski (1979). Data on modal lengths in each haul were mapped using GIS, allowing inferences to be made about growth in relation to migration patterns.

GAMs were also applied to maturity data in order to analyse patterns in relation to geographical and environmental variables. Separate models were fitted for males and females to allow identification of any differences between sexes. They were constructed following the same procedure as for the abundance model, assuming a quasi-Poisson distribution. Year was again included in the models with the aim of exploring interannual trends in squid maturity.

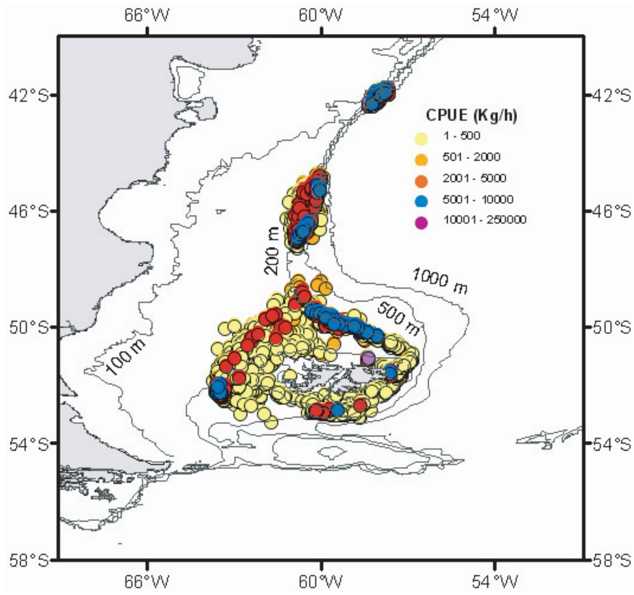

Fig. 4. Locations of observed hauls in which squid *Illex argentinus* were caught, 1988-2003, with associated catch per unit effort (CPUE, kg h^{-1}).

3 Results

3.1 Spatio-temporal distribution of *Illex argentinus* abundance

3.1.1 GIS analysis

The most consistently high catch rates for *Illex*, with CPUE > 2000 kg h^{-1} were found on the Patagonian Shelf north of 52° S during the first six months of the year (the Austral summer), with peak values higher than 5000 kg h^{-1} mainly located within 42° S, 46° S and MN areas. High catch rates were also recorded along the 200 m isobath within the Falkland conservation zones (Fig. 4). Figure 5 shows the seasonal distribution of the number of observed hauls in each fishing area.

From May to October there was a clear drop in the number of hauls that contained *Illex*. During this period, CPUE values showed a marked decrease, especially in Falkland waters where CPUE, in general, did not exceed 20 kg h^{-1}. The decrease was also pronounced in the High Seas regions where CPUE values did not exceed 1000 kg h^{-1}.

Mean November and December CPUE reached values higher than 1000 kg h^{-1}. These high-yield hauls were recorded in the 46° S region.

CPUE peaks in the first quarter of the year were observed mainly in the High Seas.

3.1.2 Generalised additive models (GAMs)

Scatter plots (Fig. 6) confirm the non-linearity of the relationships between CPUE and environmental variables. *Illex argentinus* abundance appears to be higher during the six first months of the year reaching the maximum value in May and seems to be positively related to three depth ranges: around 200, 400 and 650 m. The highest squid abundances were associated with a wide range of SST (7°–15 °C).

Table 1. Values of the Akaike Information Criterion (AIC), *p*-values and deviance explained for all possible first steps in the forward selection procedure for models of (a) presence/absence of *Illex argentinus* and (b) abundance (CPUE) of *Illex argentinus* in areas of occurrence. Initial models were constructed using those variables which explained the highest proportion of variation in the response variable. Best single explanatory variables considered are indicated by bold type.

	Presence/Absence model			Abundance (CPUE) model		
Single explanatory variable	**AIC**	***p*-value**	**Dev. Explained**	**AIC**	***p*-value**	**Dev. Explained**
Moon	1.37	0.00021	0.08%	1125.8	0.72	0.045%
Sky	1.36	$<2.22 \times 10^{-6}$	0.54%	1120.3	0.0016	0.601%
Average Depth	1.31	$<2.22 \times 10^{-6}$	4.61%	1061.3	$<2.22 \times 10^{-6}$	5.82%
SST	**1.02**	$<2.22 \times 10^{-6}$	**25.9%**	1107.7	5.55×10^{-6}	1.72%
Longitude	1.34	$<2.22 \times 10^{-6}$	2.07%	**1015.5**	$<2.22 \times 10^{-6}$	**9.88%**
Latitude	**1.03**	$<2.22 \times 10^{-6}$	**25.1%**	**1047.2**	$<2.22 \times 10^{-6}$	**7.07%**
Month	**1.05**	$<2.22 \times 10^{-6}$	**23.8%**	1082.5	$<2.22 \times 10^{-6}$	3.95%
Week	1.37	0.32	0.014%	1113.3	2×10^{-7}	1.16%
Year	1.31	$<2.22 \times 10^{-6}$	4.21%	1047.8	$<2.22 \times 10^{-6}$	7.01%

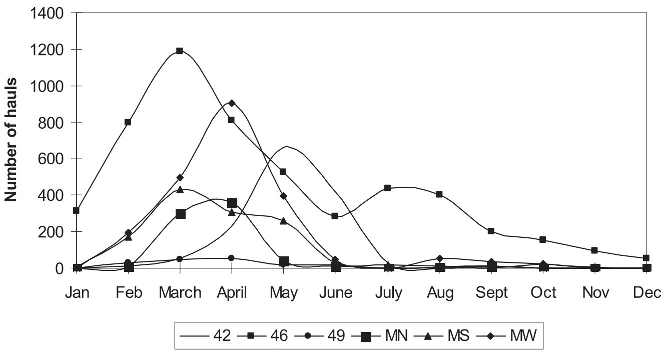

Fig. 5. The seasonal (month by month) distribution of the number of observed hauls in each fishing area.

Presence/Absence model

This model predicts the level of probability of success of catching the species. SST, latitude and month were the best explanatory variables (Tables 1 and 2) and these were used as the basis for model building.

The results indicate that the best model (with the smaller AIC value) was model 4 which included effects of SST, latitude, month, average fishing depth, year and longitude (Fig. 7, Table 3).

The probability of catching squid has been found negatively related to latitude and generally increased at higher SST values. Confidence limits tend to be wider for SST values above 15 °C, due to scarcity of data.

The presence/absence model also suggests a minimum in catches located in 1992 followed by a rapid increase to a peak in 1998. The GAM plot shows that maximum probabilities for catching *Illex* were found during March, followed by a rapid decline until the end of the year. In terms of longitude there is a peak of catches located between 59° and 58° W. In terms of average fishing depth, the probability of success of catching *Illex* is highest in depths around 600 m.

Abundance (CPUE) model

This model predicts the abundance of the species when present. The final model included effects of year, month, latitude, longitude, average fishing depth, week and SST (Fig. 8, Table 4).

Table 2. Adjusted R^2 values for each explanatory variable in the GAMs for presence/absence and abundance. R^2 was adjusted for the number of predictors in the model to avoid overestimating the strength of the association. Best single explanatory variables considered are indicated by bold type.

	Presence/Absence model	**Abundance (CPUE) model**
	R^2 (adj)	R^2 (adj)*
Moon	0.0009	−0.0004
Sky	0.0072	0.0028
Average Depth	0.0603	0.0398
SST	**0.309**	0.0082
Longitude	0.0276	**0.0567**
Latitude	**0.308**	**0.0447**
Month	**0.3**	0.0228
Week	2.7×10^{-5}	0.0067
Year	0.0558	0.0397

* Adjusted $R^2 = 1 - \dfrac{SS_{\text{residual}}/(n-(p+1))}{SS_{\text{total}}/(n-1)}$.

There is a clear increase in abundances from 1993 onwards (the maximum abundances occurring in 1999). There was also a strong seasonal effect on squid abundance. There is a decline in abundance from January to August/September and then after reaching the minimum, there is an increasing trend towards the end of the year. Regarding latitude, maximum abundances were found around 48° S and in terms of longitude there is a minimum located around 62° W. CPUE was positively related to fishing depth. *Illex argentinus* preferentially occurs in areas with SST above 10 °C.

3.2 Biological data

3.2.1 Monthly modal length

Length distributions found at 45°–46° S during January ranged between 25 and 35 cm. During the following months *Illex* migrates southwards growing rapidly. In general terms, during that period, modal length increases from 20–25 cm

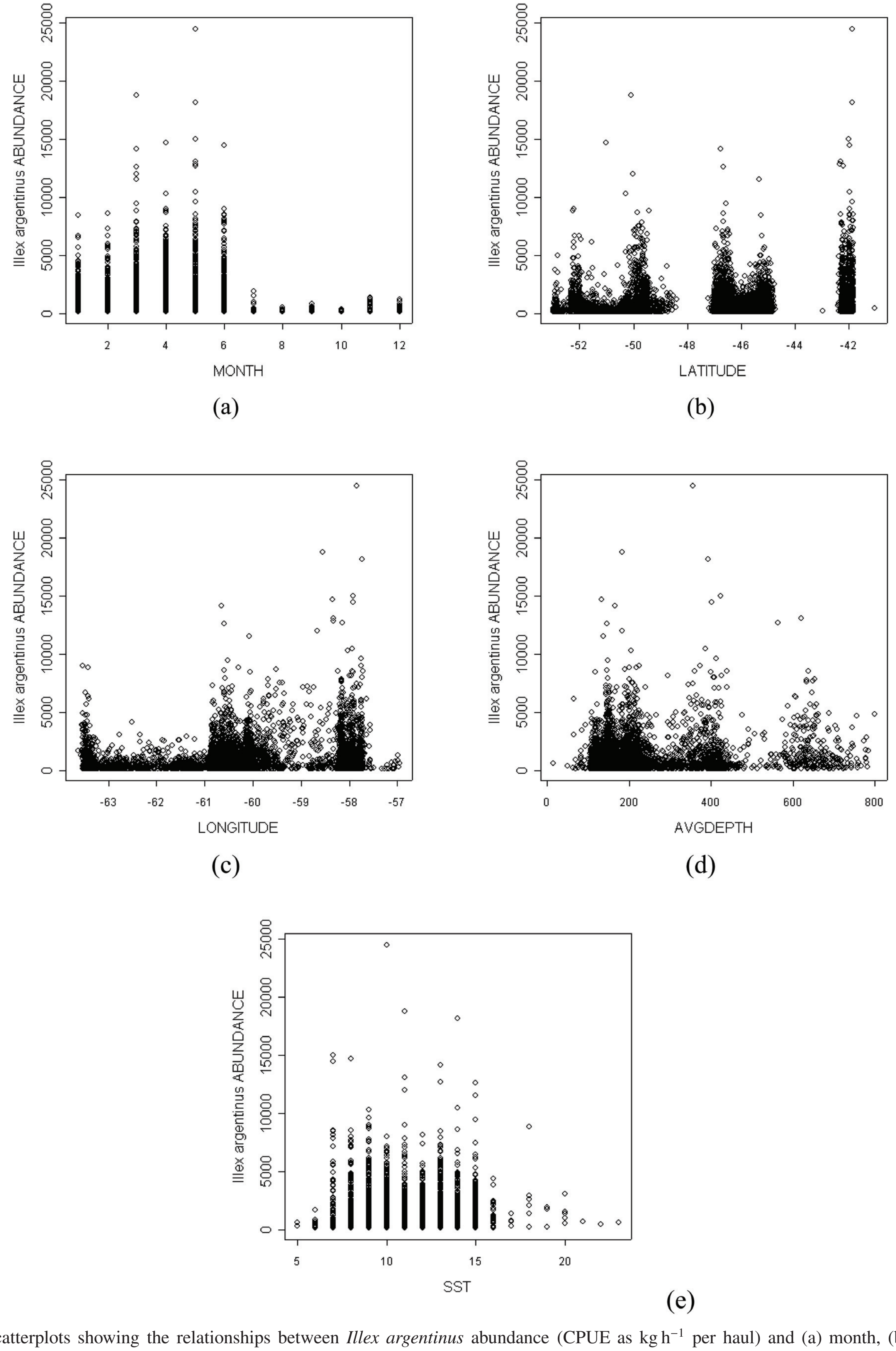

Fig. 6. Scatterplots showing the relationships between *Illex argentinus* abundance (CPUE as kg h^{-1} per haul) and (a) month, (b) latitude, (c) longitude, (d) average depth and (e) SST.

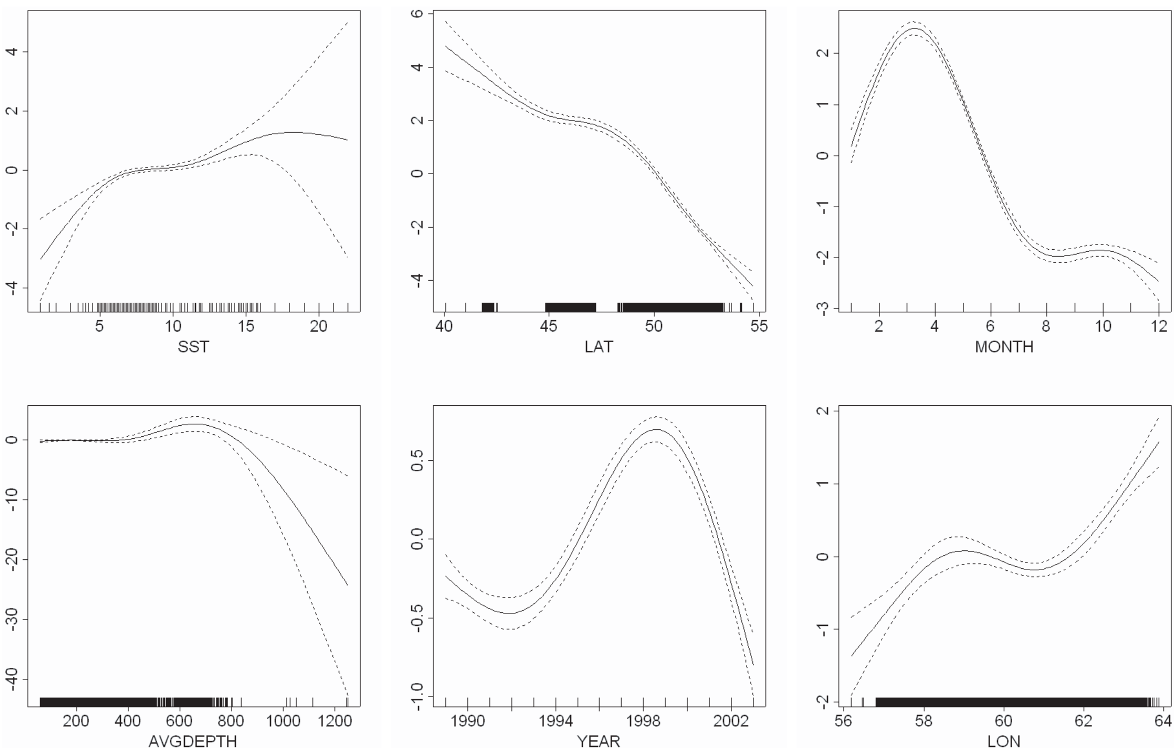

Fig. 7. Partial plots showing smoothers, with 95% confidence limits, fitted to (partial) effects of the predictor variables retained in the final (optimal) model of *Illex* presence-absence. Clockwise from top left: SST, Latitude, Month, Longitude, Year, Average fishing depth. Each variable in the model was fitted using four degrees of freedom. The model was a binomial GAM with the form: Logit(PA)~s(SST)+s(Lat)+s(Month)+s(AvgDepth)+s(Year)+s(Lon).

Table 3. Sequential goodness of fit measures associated with addition of each term to the presence/absence model. The final model considered is indicated by bold type.

	R^2 (adj)	Dev.explained	AIC
Model [1]	0.581	52.6%	0.652
Model [2]	0.583	52.9%	0.648
Model [3]	0.597	54.4%	0.627
Model [4]	**0.608**	**55.3%**	**0.616**
Model [5]	0.606	55.1%	0.619
Model [6]	0.597	54.4%	0.628

[1] PA~s(SST)+s(Lat)+s(Month)
[2] PA~s(SST)+s(Lat)+s(Month)+s(AvgDepth)
[3] PA~s(SST)+s(Lat)+s(Month)+s(AvgDepth)+s(Year)
[4] **PA~s(SST)+s(Lat)+s(Month)+s(AvgDepth)+s(Year)+s(Lon)**
[5] PA~s(Lat)+s(Month)+s(Year)+s(Lon) + SST + AvgDepth
[6] PA~s(Month)+s(Year)+s(Lon) + SST + Lat + AvgDepth.

(recorded in MS in February) to 25–30 cm (recorded in March and April in the same area) and from 25–30 cm in MW (during February) to 30–35 cm (during March and April). After this period, squid start northwards migration to spawn. Within 42° S and 46° S areas modal lengths ranged between 30–40 cm during May to July, meanwhile in August and September were characterised by the presence of 18–30 cm individuals.

Table 4. Sequential goodness of fit measures associated with addition of each term to the abundance model. The final model considered is indicated by bold type.

	R^2 (adj)	Dev. explained	AIC
Model [1]	0.0765	13%	982.5
Model [2]	0.126	20.2%	902.8
Model [3]	0.131	21.1%	895.7
Model [4]	0.156	25.9%	842.8
Model [5]	0.167	27.2%	830.1
Model [6]	**0.177**	**28.7%**	**814.1**
Model [7]	0.179	28.8%	814.2
Model [8]	0.171	28%	822.1
Model [9]	0.171	28%	821.2
Model [10]	0.169	27.6%	825.1

[1] CPUE~s(Lat)+s(Lon)
[2] CPUE~s(Lat)+s(Lon)+s(Year)
[3] CPUE~s(Lat)+s(Lon)+ s(Year)+s(AvgDepth)
[4] CPUE~s(Lat)+s(Lon)+s(Year)+s(AvgDepth)+s(Month)
[5] CPUE~s(Lat)+s(Lon)+s(Year)+s(AvgDepth)+s(Month)+s(SST)
[6] **CPUE~s(Lat)+s(Lon)+s(Year)+s(AvgDepth)+s(Month)+s(SST) +s(Week)**
[7] CPUE~s(Lat)+s(Lon)+s(Year)+s(AvgDepth)+s(Month)+s(SST) +s(Week)+s(Sky)
[8] CPUE~s(Lat)+s(Lon)+s(Year)+s(AvgDepth)+s(Month)+s(Week) +s(Sky)+SST
[9] CPUE~s(Lat)+s(Lon)+s(Year)+s(AvgDepth)+s(Month)+s(Sky) +SST+Week
[10] CPUE~s(Lat)+s(Lon)+s(Year)+s(Month)+s(Sky)+SST+Week +AvgDepth.

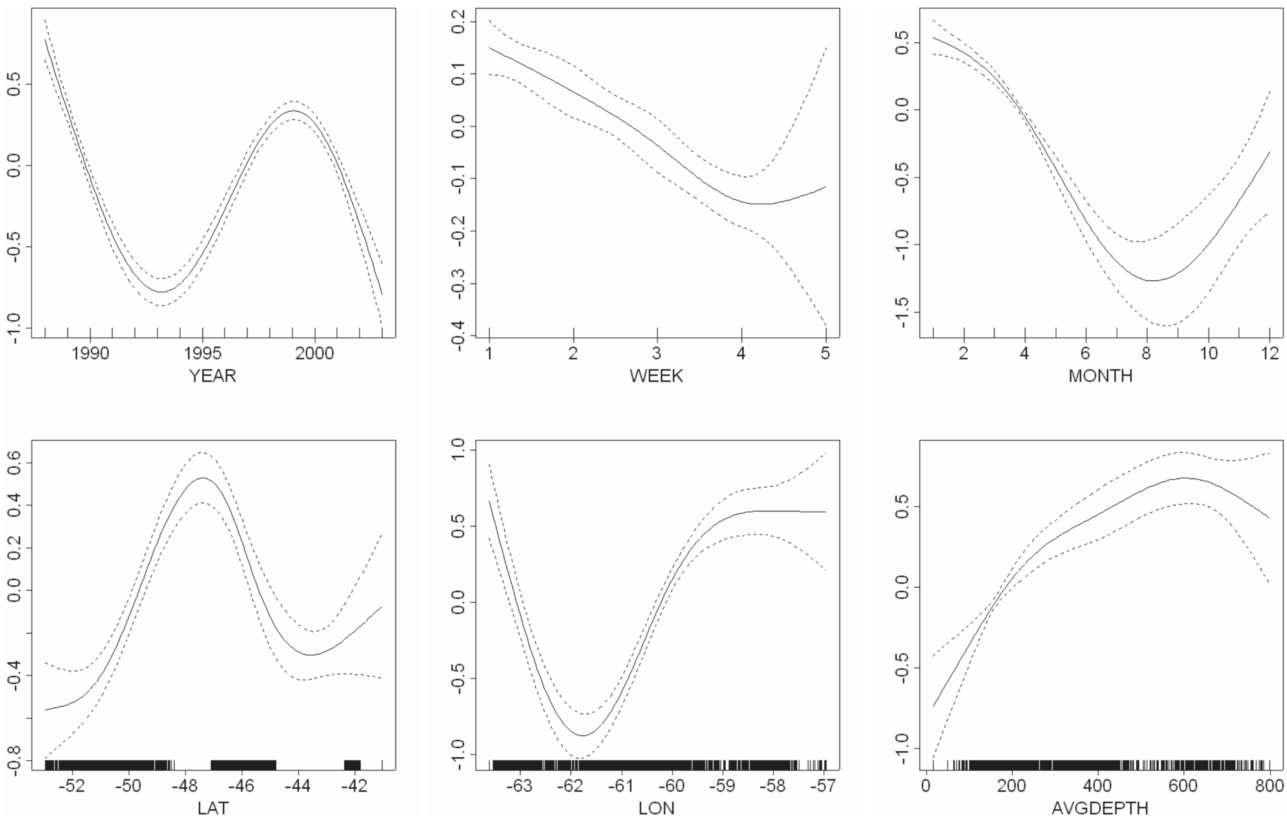

Fig. 8. Partial plots showing smoothers, with 95% confidence limits, fitted to (partial) effects of the predictor variables retained in the final (optimal) model of *Illex* abundance (CPUE) in areas of occurrence. Clockwise from top-left: Latitude, Longitude, Average fishing depth, SST. Each variable in the model was fitted using four degrees of freedom. The model was a Quasi-Poisson GAM with the form: CPUE~s(Lat)+s(Lon)+s(Year)+s(AvgDepth)+s(Month)+s(SST)+s(Week).

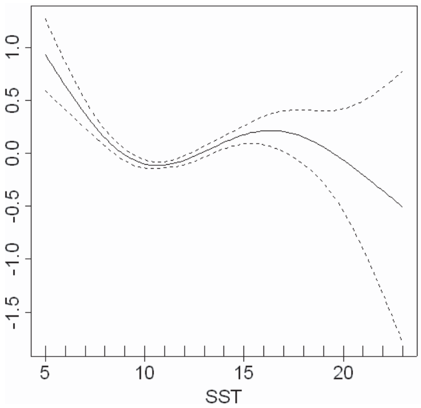

Fig. 8. Continued.

3.2.2 Maturity

From January to May there is a general increase in maturity stage for males and females (Fig. 9). During the first five months mature males dominate the sample and proportion of mature squid increases from January (48%) to May (80%). For females, during January and February immature squid dominate the sample, but the proportion of immature squid begins to decrease from March (54%) to May (22%).

During March, males were predominantly mature (mainly stages III and IV) while the modal maturity stage for females was II (immature). The maximum maturity stage found within this month was V (females). The distribution of maturity stages was rather similar in April, although the maximum maturity stage found was VI (the number of squid at this stage was negligible). In May, the majority of squid of both sexes were at maturity stage III.

3.2.3 GAM models of maturity

Best GAM fits for maturity in females and males (Figs. 10 and 11, Table 5) were observed when using temporal (year and month), geographic (latitude, longitude and average fishing depth) and environmental variables (SST).

The analysis of explanatory variables indicates that maturity increases towards the equator and peaks at latitudes between 46° S and 48° S. The model also suggests that lower maturity stages are at longitudes around 60.5° W. In terms of average fishing depth, maturity increases with depth. Regarding to SST there is a different trend for both sexes. Female maturity decreases with temperatures above 14 °C while for males maturity increases above 14 °C.

The GAM plots show, for both sexes, a clear seasonal effect on maturity, the highest maturity stages being found from February to March.

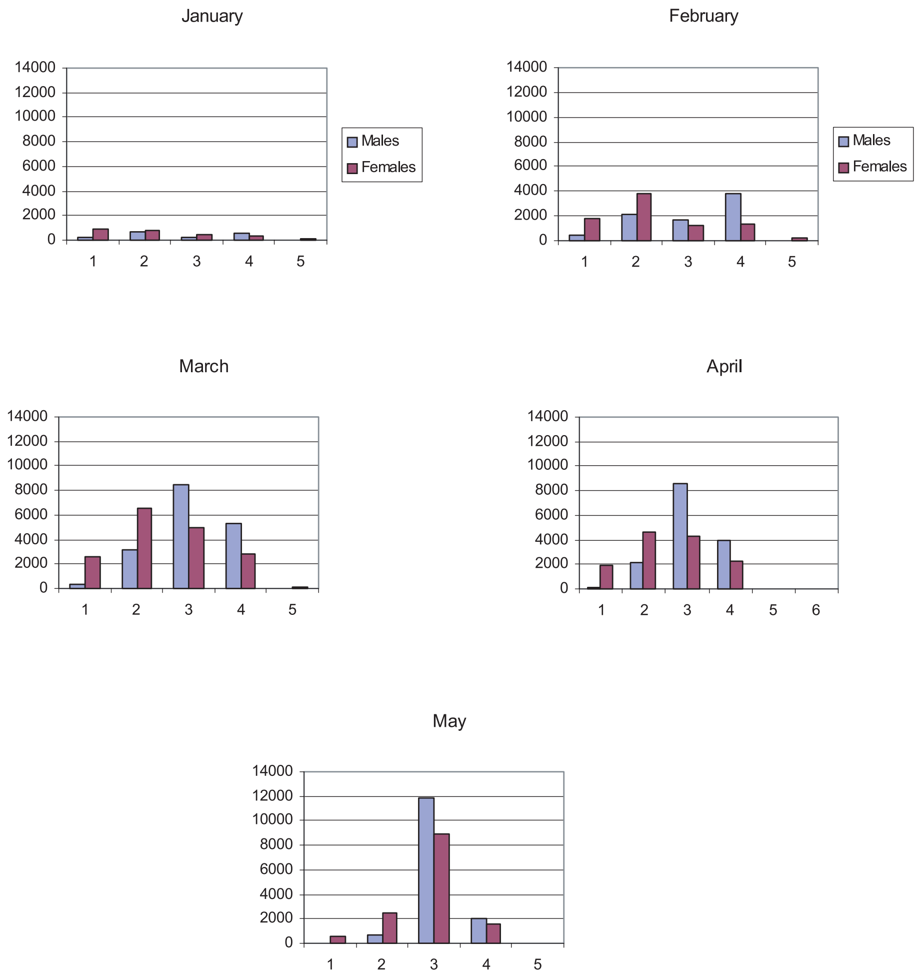

Fig. 9. Abundance (numbers caught per haul) of squid at different maturity stages on a month-by-month basis (1983-2000). Stages 3 and above are considered as mature.

4 Discussion

One of its distinguishing characteristics is that during its life-cycle, *Illex* migrates from the spawning grounds off northern Argentina, Uruguay, and Brazil southwards to the Patagonian and Falkland Islands shelves (Arkhipkin 2000). Concentrations of shortfin squid are found at 45−46° S in January or February. Peak concentrations are found around the Falkland Islands between March and May. Toward the end of this period *Illex argentinus* returns to the north where the animals spawn and die around July or August (Basson et al. 1996). The basic pattern of migration is described in Hatanaka (1988).

GIS maps obtained in this study revealed in detail information about the structure dynamics and migratory patterns of *Illex argentinus*. This information was not previously available and demonstrates the benefits of using GIS tools in determining the spatial distribution of the squid in each month as well as monthly changes. Shifts in catch distribution can help to track the recruitment, migration and spawning patterns of squid species (Caddy 1983; Pierce et al. 1998). The distribution patterns of *Illex argentinus* observed with the maps are consistent with the influx of squid migrating southward following the prey concentrations on which they are feeding (Hatanaka 1988; Brunetti and Ivanovic 1992).

As an annual species, *Illex argentinus* grows rapidly with high production to biomass ratios, but have no reserves of genetic diversity once a year class is overfished (Rodhouse et al. 1998). In this context, GIS maps have been implemented to describe the life cycle of the squid in terms of modal length distribution. Originally, *Illex argentinus* was considered to be a single stock (Sato and Hatanaka 1983; Csirke 1987; Basson et al. 1996) but further studies (Hatanaka et al. 1985; Hatanaka 1988) found that there were two populations differing both by season and place of spawning: winter and summer-spawning populations. Modal length distributions observed in October (10−15 cm) could suggest the presence of the second *Illex* generation in 46° S area (summer-spawning population). From November to December there is an evident increase in the modal length (20−25 cm) that might be explained by the growth of the summer-spawning population to continue its annual life cycle.

Squid are short-lived and their population dynamics are sensitive to environmental variation, making them suitable for the implementation of models that study the response of variables like abundance or maturity to environmental and

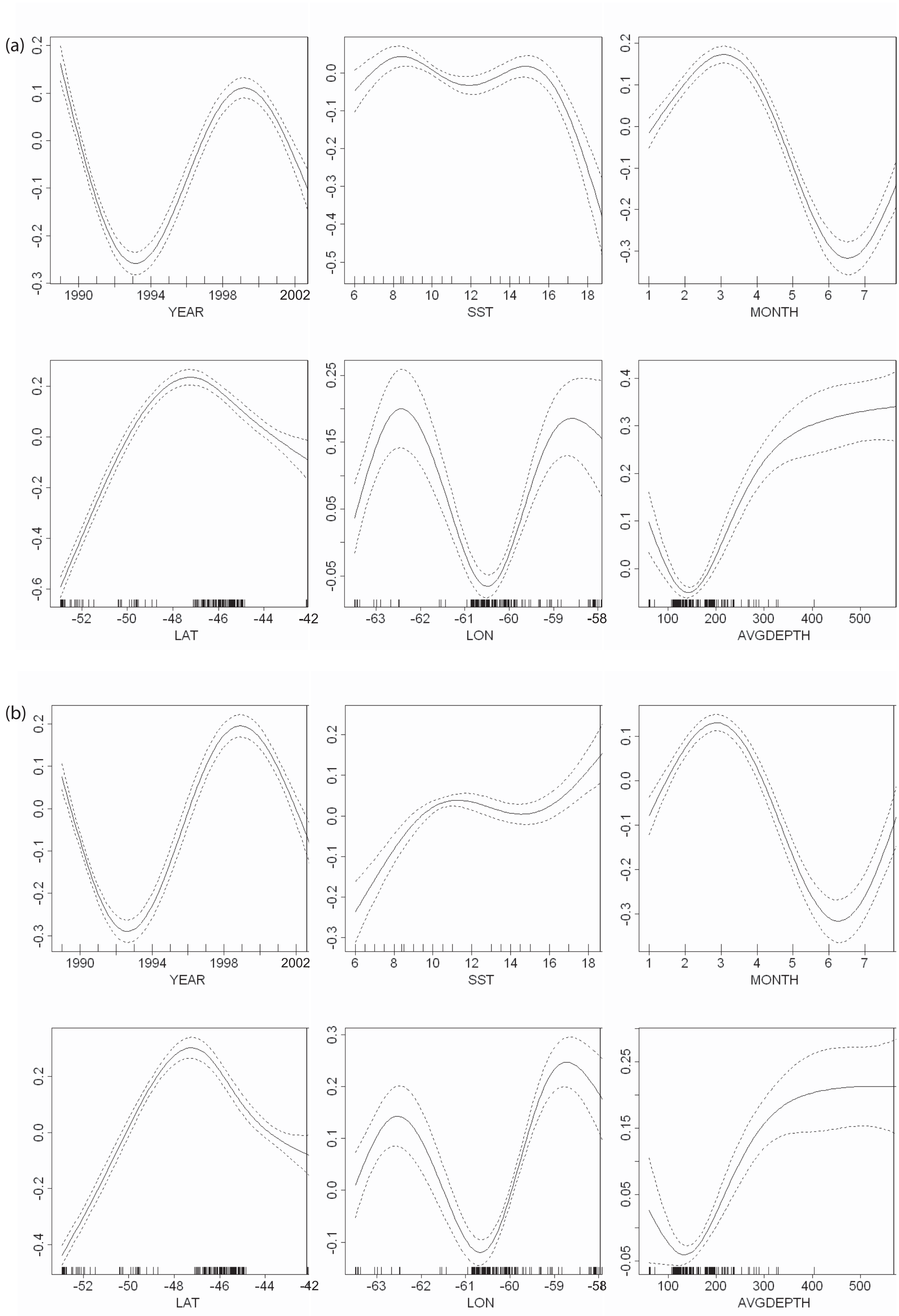

Fig. 10. Partial plots showing smoothers, with 95% confidence limits, fitted to (partial) effects of predictors in the final model of maturity stage. Clockwise from top-left: Year, SST, Month, Average depth, Longitude, Latitude. The model was a Quasi-Poisson GAM of the form: Maturity stage s(Year)+s(Month)+s(Lat)+s(Lon) +s(AvgDepth)+s(SST). (a) in females, (b) in males.

Table 5. Sequential goodness of fit measures associated with addition of each term to the model of maturity in females, and males. The final models considered are indicated by bold type.

	R^2 (adj)	Dev.explained	AIC
Females			
Model [1]	0.124	13.3%	0.31
Model [2]	0.265	28%	0.26
Model [3]	0.271	28.8%	0.26
Model [4]	0.286	30.1%	0.25
Model [5]	**0.294**	**31%**	**0.25**
Model [6]	0.298	31.4%	0.25
Model [7]	0.309	32.5%	0.24
Model [8]	0.315	33.2%	0.24
Males			
Model [1]	0.228	21.7%	0.34
Model [2]	0.389	37.9%	0.27
Model [3]	0.397	38.6%	0.27
Model [4]	0.416	40.3%	0.26
Model [5]	**0.421**	**41%**	**0.26**
Model [6]	0.423	41.3%	0.26
Model [7]	0.435	42.4%	0.25
Model [8]	0.436	42.6%	0.25

[1] Maturity ~ s(Year)+s(Month)
[2] Maturity ~s(Year)+s(Month)+s(Lat)
[3] Maturity ~s(Year)+s(Month)+s(Lat)+s(Lon)
[4] Maturity ~ s(Year)+s(Month)+s(Lat)+s(Lon)+s(AvgDepth)
[5] **Maturity ~s(Year)+s(Month)+s(Lat)+s(Lon) +s(AvgDepth)+s(SST)**
[6] Maturity ~ s(Year)+s(Month)+s(Lat)+s(Lon)+s(AvgDepth) +s(SST)+s(Moon)
[7] Maturity ~ s(Year)+s(Month)+s(Lat)+s(Lon)+s(AvgDepth) +s(SST)+s(Moon)+s(sky)
[8] Maturity ~ s(Year)+s(Month)+s(Lat)+s(Lon)+s(AvgDepth) +s(SST)+s(Moon)+s(sky)+s(week).

geographical variations. Temporal and spatial changes in the relationship between squid abundance and climatic variables have been observed by several authors (Roberts and Sauer 1994; Pierce and Boyle 2003; Pierce et al. 1998; Waluda and Pierce 1998; Robin and Denis 1999; Bellido et al. 2001). Pierce et al. (2001) investigated the relationship between cephalopod abundance and environmental factors in the North-east Atlantic. By using GAMs and GIS they found that squid CPUE tended to be positively correlated with winter SST and negatively correlated with summer SST.

Our GAM analyses indicate that environmental conditions influence the presence/absence and abundance (CPUE). Final models explained a 55.3% (PA model) and 28.7% (abundance model) of variation in the response variable. There is a strong seasonal effect in both models: maximum catchability was found during March (presence/absence model) and the maximum abundances were found during the first half of the year (abundance model).

The GAM model demonstrates that the relationship between SST and abundance is non linear the highest CPUE being found at temperatures below 10 °C. Previous work made by Waluda et al. (2001) have showed by analysis of remotely sensed SST that about 55% of variability in recruitment strength around the Falklands can be explained by variations in the optimum water temperature during the spawning season prior to recruitment.

Illex argentinus, starts to mature in about 7 or 8 months and reaches full maturity by 12 months (Rodhouse et al. 1990)

GAM models applied to maturity explained 31% (females) and 41% (males) of variation in the response variable, latitude and SST being the most important explanatory variables. Different trends for males and females were found for SST leading us to think that there may be there is some segregation by sex at high SST values. This segregation may be explained by different maturation rates in males and females (Arkhipkin 1990, 1993, 2000; Arkhipkin and Scherbich 1991).

Previous fishery studies have already used GAM techniques for spatial modelling of abundance of marine species. For example, Swartzman et al. (1992), Daskalov (1999), Denis et al. (2002) and Wang et al. (2003) used GAM to analyze geographical variations of fish and squid distribution. Bellido et al. (2001) presented a preliminary application of GAM in order to model intra-annual (spatial and seasonal) trends in squid *Loligo forbesi* abundance as function of environmental, spatial and temporal variables in Scottish waters.

The spatial representation of time series of observer data allowed visualisation of the temporal and spatial variations of CPUE for *Illex*, thus providing insight into patterns of abundance of this species in the SW Atlantic. The combination of GIS with statistical analysis methods has become an important and powerful approach for spatio-temporal analysis, understanding, prediction, and visualization of fishery resources in relation to environmental variation in spatial and temporal dimensions.

Furthermore, the pronounced interannual variations seen in squid abundance and biological traits, evident in the models even once effects of environmental variables had been removed, indicates the need for further studies to identify the causes of this variation.

The discovery of relationships between environmental-geographical variability and squid abundance may form the basis of predicting abundance in these short-lived species, with applications in fisheries forecasting and management. The models applied explained a substantial proportion of the variation in presence and abundance of *Illex* in areas where this species was recorded. They allow the evaluation of possible causal mechanisms underlying potential relationships and suggest that successful fishery forecasting is a realistic goal.

Acknowledgements. The authors wish to express their gratitude to scientific observers, crews, fishing companies and associations for their collaboration in data collection.

References

Acha E.M., Mianzan H.W., Guerrero R.A., Favero. M., Bava J., 2004, Marine fronts at the continental shelves of austral South America Physical and ecological processes. J. Mar. Syst. 44, 83-105.

Arkhipkin A.I., Scherbich Z.N. 1991, Crecimiento y estructura intraespecifica del calamar *Illex argentinus* (Ommastrephidae) en invierno y primavera en el Atlántico Sudoccidental. Scient. Mar. 55, 619-627.

Arkhipkin A. 1990, Edad y crecimiento del calamar *(Illex argentinus*). Frente Marít. 6 A, 25-35.

Arkhipkin A. 1993, Statolith microstructure and maximum age of *Loligo gahi* (Myopsida: Loliginidae) on the Patagonian shelf. J. Mar. Biol. Assoc. UK 73, 979-982.

Arkhipkin A.I., 2000, Intrapopulation structure of winter-spawned Argentine shortfin squid, *Illex argentinus* (Cephalopoda, Ommastrephidae), during its feeding period over the Patagonian Shelf. Fish. Bull. 98, 1-13.

Basson M., Beddington J.R., Crombie J.A., Holden S.J., Purchase L.V., Tingley G.A., 1996, Assessment and management techniques for migratory annual squid stocks: The *Illex argentinus* fishery in the Southwest Atlantic as an example. Fish. Res. 28, 3-27.

Bellido J.M., Pierce G.J., Wang J., 2001, Modelling intra annual variation of squid *Loligo forbesi* in Scottish waters using generalised additive models. Fish. Res. 52, 23-39.

Brunetti N.E., 1988, Contribución al conocimiento biológico-pesquero del calamar argentino (Cephalopoda, Ommastrephidae, *Illex argentinus*). Tesis, Mar del Plata, Argentina.

Brunetti N.E., Ivanovic M.L., 1992, Distribution and abundance of early life stages of squid (*Illex argentinus*) in the south-west Atlantic. ICES J. Mar. Sci. 49, 175-183.

Caddy J.F., 1983, The Cephalopods: factors relevant to their population dynamics and to the assessment and management of the stocks. In: Caddy J.F. (Ed.), Advances in Assessment of World Cephalopod Resources. FAO Tech. Pap. 231, Rome.

Csirke J., 1987, Los recursos pesqueros patagónicos y las pesquerías de altura en el Atlántico Sud-occidental. FAO, Rome Doc. Tec. Pesca. 280.

Daskalov G., 1999, Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalized additive models. Fish. Res. 41, 1-23.

Denis V., Lejeune J., Robin J.P, 2002, Spatio-temporal analysis of commercial trawler data using General Additive models: Patterns of Loliginid squid abundance in the north-east Atlantic. ICES J. Mar. Sci. 59, 633-648

Haimovici M., Brunetti N.E., Rodhouse P.G., Csirke J., Leta R.H., 1998, *Illex argentinus*. In: Rodhouse P.G., Dawe E.G., O'Dor R.K.(Eds.). Squid Recruitment Dynamics. Rome, FAO, pp. 27-58.

Hastie T., Tibshinari R., 1990, Generalized additive models. London, Chapman & Hall.

Hatanaka H., Kawahara S., Uozumi Y., Kasahara S., 1985, Comparison of live cycles of five ommastrephid squids fished by Japan: *Todarodes pacificus*, *Illex illecebrosus*, *Illex argentinus*, *Nototodarus sloani sloani* and *Nototodarus sloani gouldi*. NAFO Sci. Counc. Stud. 9, 59-68.

Hatanaka H., 1986, Growth and life span of short-finned squid *Illex argentinus* in the waters off Argentina. Bull. Jpn. Soc. Sci. Fish. 52, 11-17.

Hatanaka H., 1988, Feeding migration of short-finned squid *Illex argentinus* in the waters off Argentina. Nippon Suisan Gakkaishi 54, 1343-1349.

Lipinski M. 1979, Universal maturity scale for the commercially important squids. The results of maturity classification of the *Illex illecebrosus* population for the years 1973–77. Int. Comm. Northwest Atlantic Fisheries, Res. Doc. 79/2, 38, Ser. 5364.

Martos P., Piccolo M.C., 1988, Hydrography of the Argentine continental shelf between 38° and 42° S. Cont. Shelf Res. 8, 1043-1056.

McCullagh P., Nelder J.A., 1989, Generalized Linear Models. Chapman and Hall, London.

Nesis K.N., 1987, Cephalopods of the world. Neptune City, TFH Publications. p. 351.

Pierce G.J., Boyle, P.R., 2003, Empirical modelling of interannual trends in abundance of squid (*Loligo forbesi*) in Scottish waters. Fish. Res. 59, 305-326.

Pierce G.J., Wang J., Bellido J.M., Robin J.P., Denis V., Koutsoubas D., Valavanis V., Boyle P.R., 1998, Relationship between cephalopod abundance and environmental conditions in the northeast Atlantic and Mediterranean as revealed by GIS. ICES CM 1998/M:20.

Pierce G.J., Wang J., Zheng X., Bellido J.M., Boyle P.R., Denis V., Robin J.-P., 2001, A cephalopod fishery GIS for the Northeast Atlantic: Development and application. Int. J. Geogr. Inform. Sci. 15, 763-784.

Portela J.M., Arkhipkin A., Agnew D., Pierce G., Fuertes J.R., Otero M.G., Bellido J.M., Middleton D., Hill S., Wang J., Ulloa E., Tato V., Cardoso X.A., Pompert J., Santos B., 2002, Overview of the Spanish fisheries in the Patagonian Shelf. ICES CM 2002/L: 11.

Roberts M.J., Sauer W.H.H., 1994, Environment: the key to understanding the South African chokka squid (*Loligo vulgaris* reynaudii) life cycle and fishery ? Antarct. Sci. 6, 249-258.

Robin J.P., Denis V., 1999, Squid stock fluctuations and waters temperature: temporal analysis of English Channel Loliginidae. J. Appl. Ecol. 36, 101-110.

Rodhouse P.G., Hatfield E.M.C., 1990, Dynamics of growth and maturation in the cephalopod *Illex argentinus* (Teuthoidea: Ommastrephidae). Phil. Trans. R. Soc. Lond. B. 344, 201-212.

Rodhouse P.G., Barton J., Hatfield E.M.C., Symon C., 1995, *Illex argentinus*: life cycle, population structure and fishery. ICES Mar. Sci. Symp. 199, 425-432.

Rodhouse P.G., Dawe E.G., O'Dor R.K., 1998, Squid recruitment dymanics. The genus *Illex* as a model. The commercial *Illex* species. Influences on variability. FAO Fish. Tech. Pap. 273.

Santos R.A., Haimovici M., 1997, Reproductive biology of winter-spring spawners of *Illex argentinus* (Cephalopoda: Ommastrephidae) Brazil. Scient. Mar. 61, 53-64.

Sato T., Hatanaka., 1983, A review of assessment of Japanese distant-water fisheries for cephalopods. In: Caddy J.F. (Ed.), Advances in assessment of world cephalopod resources. FAO Fish. Tech. Pap. 231, pp. 14-180.

Swartzman G., Huang C., Haluzny S., 1992, Spatial analysis of Bering Sea groundfish survey data using generalized additive models. Can. J. Fish. Aquat. Sci. 49, 1366-1379.

Swartzman G., Silverman E., Williamsom N., 1995, Relating trends in walleye Pollock (*Theragra halcogramma*) abundance in the Bering Sea to environmental factors. Can. J. Fish. Aquat. Sci. 52, 369-380.

Waluda C.M., Pierce G.J., 1998, Temporal and spatial patterns in the distribution of squid (*Loligo* spp.) in UK waters. S. Afr. J. Mar. Sci. 20, 323-336.

Waluda C.M., Trathan P.N., Rodhouse P.G., 1999, Influence of oceanographic variability on recruitment in the *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. Mar. Ecol. Prog. Ser. 183, 159-167

Waluda C.M., Rodhouse P.G., Trathan P.N., Pierce G.J., 2001, Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. Fish. Oceanogr. 10, 207-216.

Wang J., Pierce G.J., Boyle P.R., Denis V., Robin J.P., Bellido J.M., 2003, Spatial and temporal patterns of cuttlefish (*Sepia officinalis*) abundance and environmental influences: a case study using trawl fishery data in French Atlantic coast, English Channel, and adjacent waters. ICES J. Mar. Sci. 60, 1149-1158.